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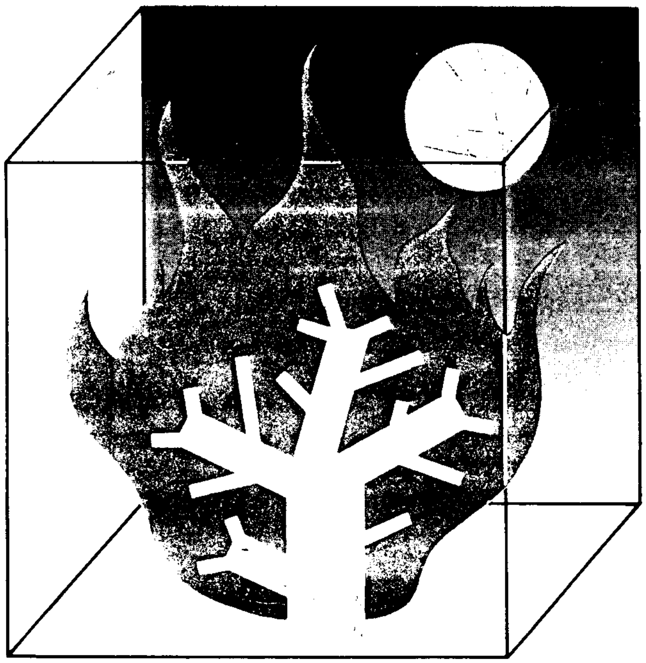

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FORTY YEARS OF PRESCRIBED BURNING ON THE SANTEE FIRE PLOTS: EFFECTS ON UNDERSTORY VEGETATION

David L. White, Thomas A. Waldrop, and Steven M. Jones[1]

Abstract—The effects of 43 years of repeated prescribed burning on crown cover, species composition, species richness, and diversity in the lower understory strata of the Santee Fire Plots were examined. Five study treatments, installed in 1946, include an unburned control, periodic winter and summer burns, and annual winter and summer burns. Understory cover has not changed in the past 20 years except in the annual winter burn plots where cover of trees $\leq$ 1.5 m in height declined and grass cover increased. Detrended correspondence analysis indentified four distinct understory plant communitites corresponding to season and frequency of burn. Distribution of understory species across a fire disturbance gradient is discussed in terms of varying plant adaptations to fire. Species richness, when separated into herbaceous and woody species groups, and Shannon's diversity index varied significantly across treatments.

INTRODUCTION

The Santee Fire Plot (SFP) study in the Francis Marion National Forest provides a unique opportunity to examine the response of understory vegetation to long-term use of several combinations of season and frequency of burning. Several studies have examined the effects of single or repeated prescribed fires on understory vegetation (Abrahamson 1984; Conde and others 1983; Cushwa and others 1966, 1969; DeSelm and others 1974; Fox and Fox 1986; Gilliam and Christensen 1986; Grano 1970; Grelen 1975; Hodgkins 1958; Lemon 1949, 1967), but none of these studies was conducted over a period as long as the period of the SFP study. Prescribed burning in loblolly pine stands on the SFP was initiated in 1946 and continued without interruption until 1989, when the overstory pines were destroyed by Hurricane Hugo.

Previous SFP studies focused on the effect of prescribed fire on understory vegetation (Langdon 1971, 1981; Lewis and Harshbarger 1976; Lotti 1955, 1956; Lotti and others 1960), benefits to wildlife (Lewis and Harshbarger 1976) and soil chemical changes (Wells 1971; McKee 1982). Waldrop and others (1987) summarized the effects of the various treatments on the growth of overstory pines after 40 years. Lewis and Harshbarger (1976) reported the effects of prescribed fire on shrub and herbaceous vegetation in the plots after 20 years. On the basis of information developed by Lewis and Harshbarger (1976), Langdon (1981), Waldrop and others (1987), and Waldrop and Lloyd (1991), the following generalizations can be made regarding the effects of long-term use of prescribed fire on understory vegetation in the SFP: (1) the unburned control plots were dominated by several size classes of shrub and hardwood species and contained only small numbers of grasses and virtually no forbs; (2) plots that were burned periodically contained two distinct size classes of understory hardwoods (>15 cm and <5 cm d.b.h.) and herbaceous species, most of which were grasses; (3) annual winter and biennial summer burns resulted in large numbers of woody stems < 1 m tall and many grasses and forbs; and (4) annual summer burning virtually eliminated understory woody vegetation, and produced an understory dominated by grasses and forbs.

This paper describes differences among plant communities in the Santee Fire Plots after 43 years of prescribed burning. More specifically, we compare the understory plant communities in the context of plant species composition, species richness, and diversity. We also sought to determine whether there have been any changes in understory species composition since year 20 (1967).

METHODS

Site Description

The SFP study was originally designed with three replications on the Santee Experimental Forest in Berkeley County, SC, and two replications on the Westvaco Woodlands in Georgetown, SC. The Westvaco plots were regenerated in 1984 so the present study is confined to the three Santee replications. Study plots are located on the upper terrace of the coastal flatwoods region of the Flatwoods Coastal Plain Province, at an elevation of 9.0 m above sea level (Meyers and others 1986). They contain a variety of soil series, which are generally described as poorly drained Ultisols of medium to heavy texture.

Study Design

The SFP study was initiated in 1946 in 42-year-old naturally regenerated loblolly pine with a well-developed understory of hardwoods (post oak, blackjack oak, southern red oak,

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dogwood, American holly, miscellaneous hickories, sweetgum, and blackgum) and shrubs (bayberry, pepperbush, and gallberry). Initially, five treatments were installed: (1) no-burn control, (2) periodic winter burn, (3) periodic summer burn, (4) annual winter burn and (5) annual summer burn. An additional treatment, biennial summer burn, was installed in 1951. Because of recent insect-related mortality in some plots of the biennial summer burn, it was not included in this study.

Winter burning was conducted as soon as possible after December 1 of each year when the temperature was 16 °C (60 °F) or higher. Summer burning was conducted after June 1 when the temperature was 32 °C (90 °F) or higher. Burning was conducted only when relative humidity was less than 50 percent, wind speed was 1 to 7 mi/h and fuel moisture was < 10 percent. Backing fires were used initially; later, head fires (strip and flanking) were used in the annual burn plots. Periodic burns were conducted when 25 percent of the understory stems reached 2.5 cm dbh. The average burn interval for periodic burns was 5 years. More detailed site descriptions can be found in Lotti (1960) and Waldrop and others (1987).

For sampling understory vegetation, a 25- by 25-m sample plot was established within each of the 32- by 32-m treatment plots. Two 25-m line transects were randomly located in each sample plot to determine percent crown cover for the following species groups: grasses, legumes, other herbs, woody vines, shrubs, and trees. The vegetation sampled in this study was the lower understory, which was defined as plants $\leq$ 1.5 m tall or plants having a majority of their crown at or below a height of 1.5 m. Cover was determined along a 25-m line transect by measuring the portion of a crown intersected by the 25-m line. Where two or more crowns overlapped, the overlapping sections of the lower crown(s) were not included.

Two 0.5- by 2-m subplots were randomly located along each 25-m transect (four subplots per plot) to measure stem density or abundance. All plants were identified to species or genus and the number of plants per species or genus was recorded. In measuring abundance of plants that sprout from roots or rhizomes, no attempt was made to determine whether a clump of stems was associated with just one individual or many. Species not encountered in the four subplots were tallied in two 1- by 25-m subplots, each of which was located adjacent to a 25-m transect. The larger subplots (1- by 25-m) were used primarily to sample relatively uncommon species. Species not encountered in subplots of either size but occurring in a 25- by 25-m sample plot were listed as present but not tallied. The species and density data were used to determine species diversity and richness.

Data Analysis

Analysis of variance was used to test for significant treatment and block effects on species richness and diversity. Mean separation was by Fisher's unprotected LSD test (Statistical Analysis System (SAS) 1987). Species richness is the total number of species in a given area. The Shannon-Weaver index was used as a measure of species diversity and was calculated as:

$$H^{\prime} = -\sum(p_i \ln p_i)$$

where p_i=proportion of individuals of species i to the total number of individuals of all species (base e logarithms are used here).

Detrended Correspondence Analysis (Gauche 1982; Hill 1979; Hill and Gauche 1980) was used to interpret the variation in vegetation composition among treatments. The technique groups plots or communities based on similarity of species composition and relative abundance. The degree of difference between plots is indicated by standard deviation (S.D.) units. A separation of communities by four S.D. units generally indicates that the two communities have no species in common, while one S.D. unit indicates approximately a 50-percent difference in species composition (Hill 1979; Hill and Gauche 1980).

RESULTS AND DISCUSSION

Changes in Understory Cover Between 1967 and 1989

Lewis and Harshbarger (1976) reported on the status of herbaceous and shrub vegetation after 20 years of prescribed burning on the SFP. We chose to compare percent cover by species group at year 43 with their data to determine whether vegetation changes had occurred since their 1967 study. Only the no-burn, periodic summer, and annual winter treatments were compared, because the interval between burning and sampling was not always the same in both studies.

In the no-burn treatments (fig. 1a), both shrub and tree cover declined over the 23-year period. Some trees and shrubs formerly in the understory grew into the midstory. Also, midstory hardwoods that were present in 1967 continued to grow, further reducing the amount of light reaching the forest floor.

In the periodic summer burn plots (fig. 1b), there were few changes between years 20 and 43. At both times, the understory was dominated by shrubs and trees. A slight increase in total cover (all species) may have been caused by increased sprouting of trees and shrubs (Langdon 1981).

Greater changes were observed in the annual winter burn plots (fig. 1c). From year 20 to year 43, tree cover declined and grass cover increased. Little change was observed for the other species groups. Although tree cover declined, the number of hardwood stems (44,700 stems ha^{-1}) was similar to

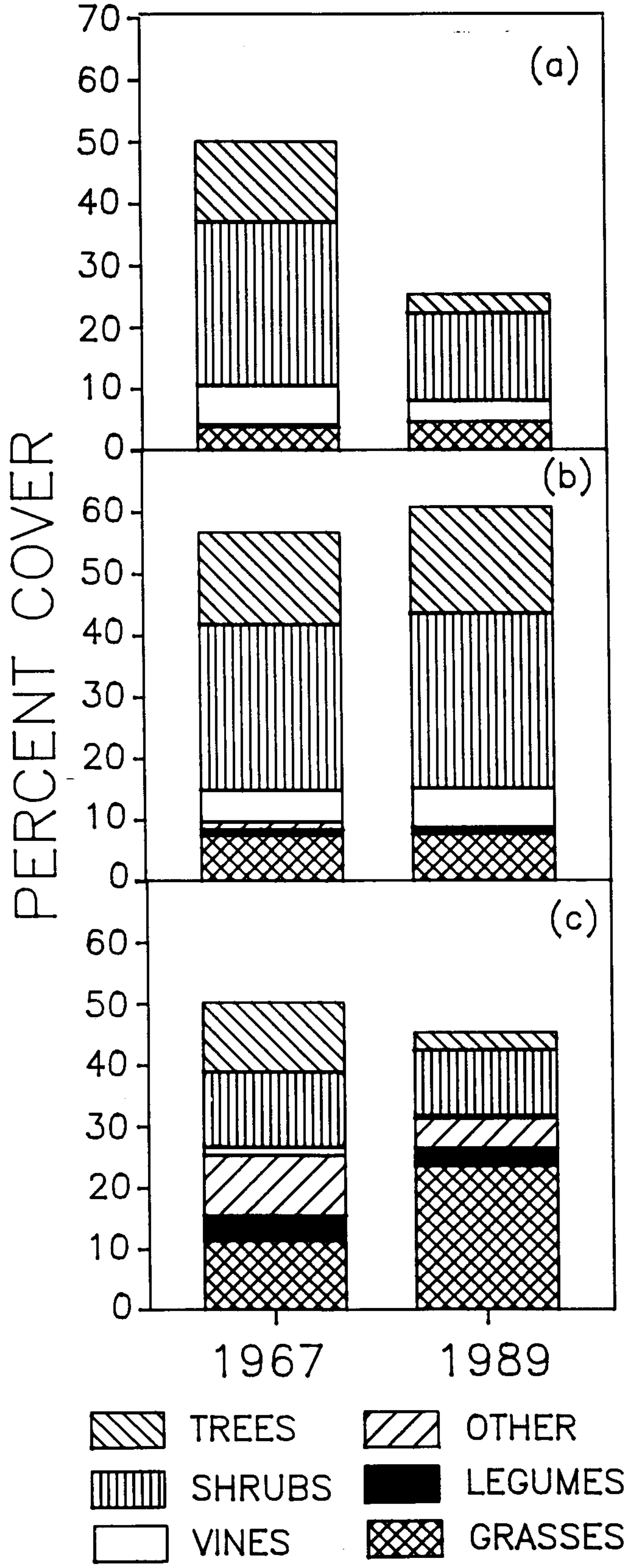

Figure 1–Understory cover by treatment, 1967 and 1989. Treatments: (a) no-burn control, (b) periodic summer burn, (c) annual winter burn. 1967 data are from Lewis and Harshbarger (1976).

the number reported by Langdon (1981) at year 30 (47,000 stems ha^{-1}). This pattern suggests that hardwood sprouts are smaller than before and that frequent winter burning may reduce sprout vigor over time. The increased importance of grasses in these plots may be a response to the decline in tree cover or it may have contributed to that decline. While the majority of vegetation changes in annual winter burn plots occurred early in the SFP study, our results indicate that the frequent but relatively mild disturbance associated with this treatment continues to cause changes in vegetation over extended periods of time.

Plant Community Differences

Community Analysis

Detrended correspondence analysis identified four distinct vegetative communities that were associated with season and frequency of burning (fig. 2). Annual summer burns, annual winter burns, periodic burns, and no-burn controls produced distinctive communities. Differences between treatments were less distinct for the periodically burned plots and the control plots, where woody vegetation predominated. The understory communities produced by periodic winter and summer burning were very similar. The distribution of plots along the X axis leads us to interpret this axis as a fire-mediated disturbance gradient. The relatively large magnitude of difference across treatments (3.5 S.D. units) indicates that beta diversity, or between-community diversity, is high and is affected by season and frequency of burning. Separations along the Y axis are less easily understood, but are interpreted as representing a natural variability gradient. Variability in species composition within a community type decreases as the level of burning increases.

The distribution of species along a fire disturbance gradient reflects the species fire tolerance and competitive vigor. Table 1 is a species synthesis table, as described by Mueller-Dombois and Ellenburg (1974), showing the relative abundance of each species in each treatment plot. This list has been edited to contain only differential species, or those species that demonstrate clear associations for a given treatment or treatments. The 32 species in this table were placed in 5 groups based on their affinity for a given treatment or treatments. Detrended correspondence analysis indicated that the periodic winter and summer burn plots were vegetatively similar and since our sampling of the vegetation took place during the growing season following the burning of the periodic winter plots, only the periodic summer burn treatment is shown in table 1.

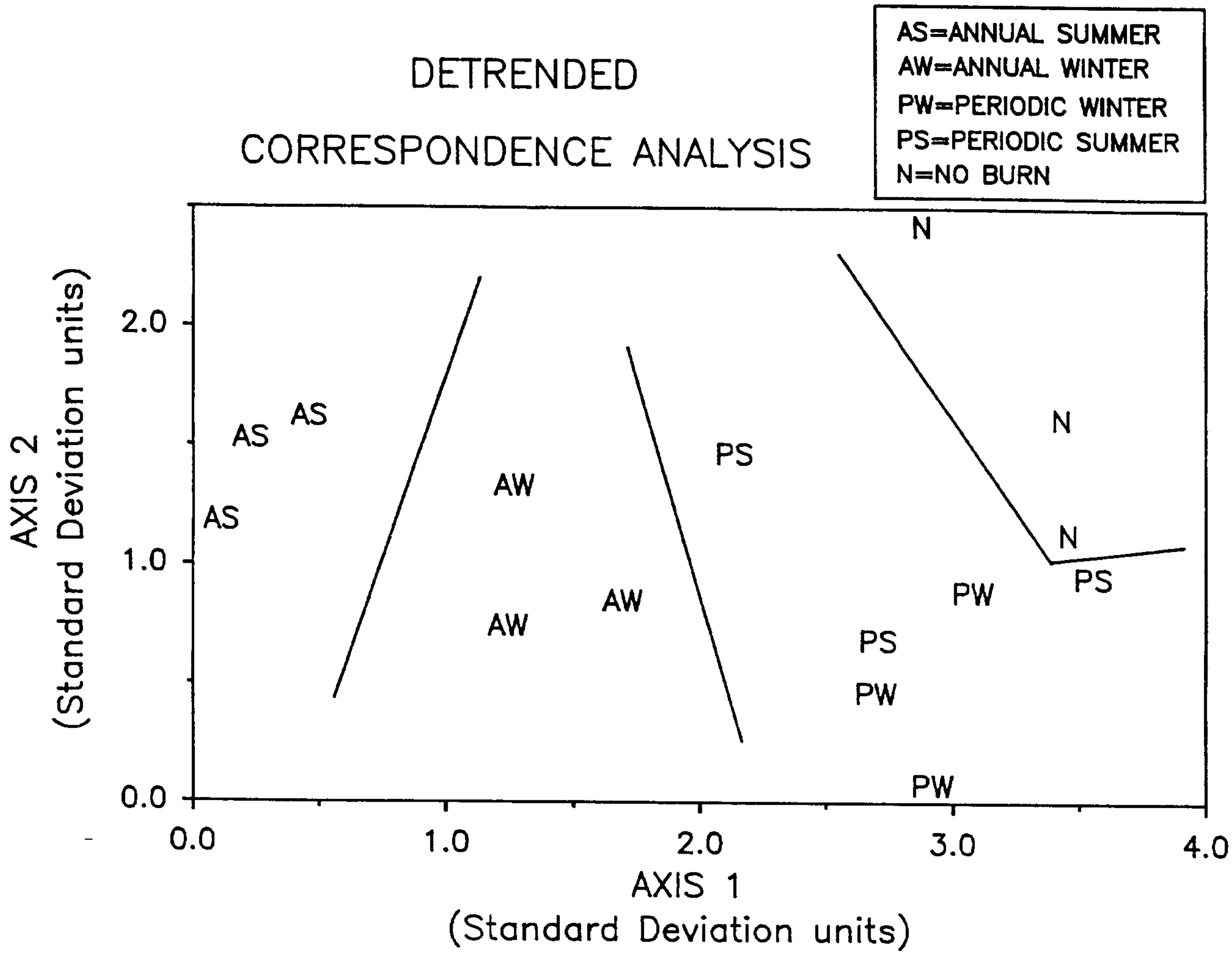

Figure 2--Results of detrended correspondence analysis of all understory plants in all treatment plots. Treatments indicated by the following codes: AS=annual summer burn, AW=annual winter burn, PS=periodic summer burn, PW=periodic winter burn, N=no-burn control. Lines are drawn to show separation between dissimilar groups of plots. See text for explanation of axes.

With few exceptions, groups 1, 2, and 3 are herbaceous plants that have been described as "fire followers" (Lemon 1949, 1967). Many of these plants are also associated with early successional plant communities following non-fire disturbance. Other species, such as the legumes, are known to benefit directly from the effects of fire (Cushwa and others 1969; Martin and Cushwa 1966; Martin and others 1975). The species in group 1 are found almost entirely in the annual summer burn plots. These are generally opportunistic species that lack the competitive vigor to become established in other burned plots, where more vigorous grasses and woody plants predominate. Species in group 2 are most common in the annual winter burn plots, but some of the legume species are also common in the periodic summer or annual summer burn plots. Generally, group 2 species are less tolerant of annual summer burning and do not compete well with the hardier woody vegetation characteristic of the periodically burned plots. The relatively low abundance of legumes in plots that have been burned every summer may result from the lack of full growing seasons in which to partition photosynthate into perennial rootstocks. Plants in group 3 were common in all burned plots but absent in the no-burn control plots, indicating a dependence on frequent disturbance. Four composite species, two grasses (Panicum species and Andropogon virginicus), and three woody plants (Hypericum species, Rubus species, and Rhus coppalina) comprised this group. Most species in group 3 disperse their seed broadly and compete vigorously for resources and this enables them to become established quickly after fire.

Groups 4 and 5 (table 1) contain all woody plants with the exception of one grass (Uniola laxa) and one perennial (Mitchella repens). Most of the species in this group reproduce vegetatively - but with varying degrees of vigor, as is indicated by the absence of some species from either the annually or periodically burned plots. Group 4 species are relatively abundant in all but the annual summer plots, maintaining their abundance primarily through vegetative reproduction. About half of these species occurred rarely or infrequently in the annual summer plots; however, their occurence in the annual summer plots is probably due to germination from seed that was transported to the plot by

Table 1--Species synthesis table showing relative abundance[a] of each species across treatments (three plots per treatment)

		Treatment											
Species[b]	Group	Unburned control			Periodic summer			Annual winter			Annual summer		
Paspalum species	1										9	R	
Polygala lutea											9	R	3
Hypoxis micrantha										R	1	9	7
Rhexia species									R	+	9	R	R
Coreopsis major	2							+	9	1	+		
Cassia nictitans								5		5	9		
Stylosanthes biflora								4	1	8	4	9	
Galactia macreei								9		1			
Desmodium species							2	+		9	+	R	
Tephrosia hispidula					R		R		R	9	1		
Centrosema virginianum					R		R	9		9			
Lespedeza species						+	+	+	+	9			
Lobelia nuttallii	3				+				9	R	+	6	4
Aster species					1			1	9	2	1	+	+
Solidago species					+		R	9	+	4	2	1	
Eupatorium species					+	+	R	8	9	7	2	3	+
Elaphantopus species					+		+	9	+		1	1	+
Panicum species					3	+	1	6	9	3	6	2	3
Andropogon virginicus					+		+		6	9	5	9	3
Hypericum species					+		8		8		+	2	1
Rubus species				1	4	5	5	+	1	5	+	R	
Rhus coppalina			+		+		R	2	R	1	1	R	R
Pinus taeda	4		+	1	8	+	+	R	+	+	7	9	6
Gaylussacia species		+	+	+	+	3	1	+	1	4	R		+
Vaccinium species			1	+	1	1	6	+	3	9	+		+
Uniola laxa		+	+	+	3	+	+	9	3	5			+
Myrica cerifera		1	+	+	9	2	1	1	R		+		
Liquidambar styraciflua		+	+	+	5	1	+	4	1	9			
Smilax species		9	1	1	2	+	R	1	+				
Vitis species		+	1	+	1	1	+	+		+	R		
Quercus species		+	+	+	6	4	3	+		9			+
Gelsemium sempervirens		+	+	+	7	9	1				+		+
Cornus florida	5		3	2	7	8	9				R		
Mitchella repens			4	+	3	9	2						
Persea borbonia		9	+	+			R						
Lyonia lucida			+	9									

[a] Relative abundance indicated as deciles:"+"=1-10 percent of the maximum abundance value for a given species,"1"=11-20 percent; etc. "R" indicates that a species was rare in the vegetation plot (i.e., was present only).
[b] Nomenclature follows Radford and others (1968).

wind or animals. Species in group 5 were relatively intolerant of frequent burning. Cornus florida (dogwood) and Mitchella repens (partridge berry) were absent from annual burn plots, while Persea borbonia (redbay) and Lyonia lucida (fetterbush) were absent from both periodic and annual plots. Fetterbush has been previously mentioned as one of several shrubs on the SFP that sprout prolifically after fire (Langdon 1981). Data from other studies (Cypert 1973; Abrahamson 1984) also suggest that this species is tolerant of fire. The absence of this species in year 43 may indicate that the species is intolerant of long-term frequent burning, at least on sites similar to those in the SFP study area.

Species Abundance

Understory species abundance (number of plants 0.1 ha^{-1}) for woody plants is shown in figure 3. Abundance of hardwoods, shrubs, and vines was dramatically reduced by annual summer burning. In the periodic burn plots and the annual winter burn plots, understory hardwood abundance was slightly greater than in unburned controls. Only the annual summer burn plots had lower shrub abundance than the control plots. The large values for shrubs are attributable primarily to the rhizomatous shrubs, Gaylusaccia spp. (Huckleberry) and Vaccinium spp. (blueberry), which sprout prolifically after fire. The greater abundance of all three woody plant groups in periodic winter burn plots was due to the fact that these plots had been burned the winter prior to sampling, which illustrates the immediate response to fire by this predominantly woody understory.

Abundance of grasses, legumes, and other forbs is shown in figure 4. Herbaceous plant abundance increased with increasing fire frequency, and abundance of all three groups was greatest in the annual winter burn plots. The annual winter treatment yielded a substantially higher number of legume stems than all the other treatments. Legume abundance in the annual winter burn plots was higher than values reported from other studies in the South (Buckner and Landers 1979; Cushwa and Jones 1969; Cushwa and others 1970, 1971; Hendricks 1989; Speake and others 1975). Legume abundance in the periodic and the annual summer burn plots was in the range found in the studies cited above, most of which were conducted after single or periodic burns.

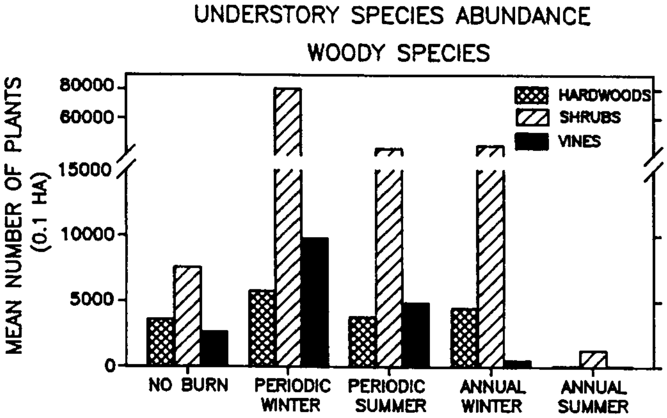

Figure 3--Mean number of stems 0.1 ha^{-1} for understory woody plant groups across all treatments. Note axis scale change.

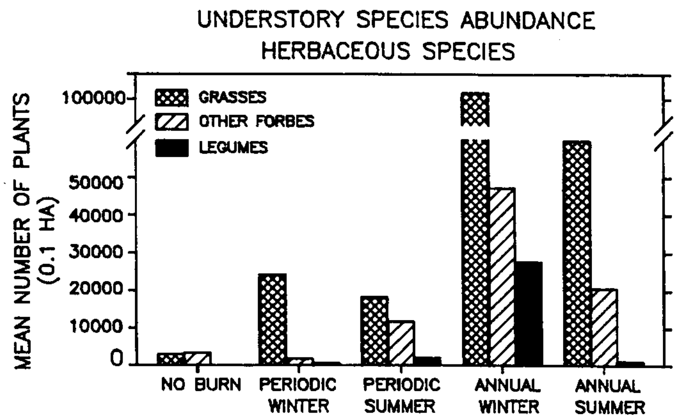

Figure 4--Mean number of stems per 0.1 ha^{-1} for understory herbaceous plant groups across all treatments. Note axis scale change.

Species Richness and Diversity

Understory species richness was not significantly affected by treatment. When species richness was separated into woody and herbaceous categories, treatment effects were significant (fig. 5). Woody species richness was significantly higher for the no-burn and periodic burn treatments than for either of the annual burn treatments. In contrast, herbaceous species richness increased with increasing burning frequency and was significantly higher for the annual winter burn treatment than for the periodic winter and the no-burn treatments.

Shannon diversity, calculated using all understory species, was significantly affected by treatment (table 2). Understory species diversity was significantly higher for the annual winter burn treatment than for the annual summer and periodic winter burn treatment but not higher than for the periodic summer and no-burn treatments. It is significant that differences in richness and diversity among treatments were not more distinct. As burning frequency increased, herbaceous species importance increased and there was an associated decline of woody species. This species replacement resulted in relatively small differences in diversity and richness between most treatments. Annual winter burning resulted in higher richness and diversity values because woody biomass was reduced to a level sufficient to allow establishment of herbaceous plants, many of which responded positively to the conditions created by fire.

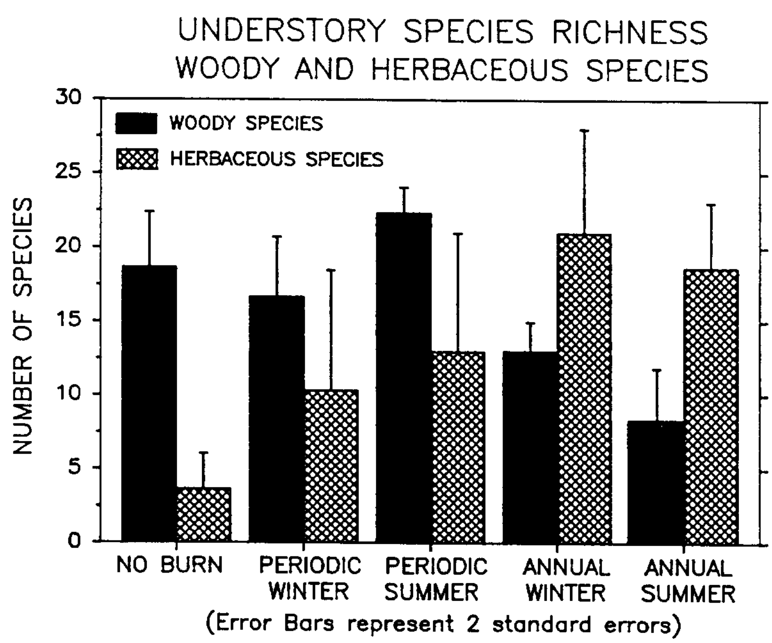

Figure 5--Understory species richness. Error bars represent two standard errors.

Table 2--Shannon diversity indices for understory plant communities from each treatment

Treatment	Diversity Index[a]
Annual winter burn	2.40 a
Periodic summer burn	2.28 ab
No burn control	2.07 abc
Annual summer burn	1.88 bc
Periodic winter burn	1.70 c

[a] Means with different letters are significantly different at the 0.05 level.

CONCLUSIONS

While all plants in this southern pine ecosystem are well adapted to fire, it is the fire regime--incorporating intensity, frequency, and season--rather than fire itself, to which plant species are adapted (Gill 1975). Observed differences in species composition of understory plant communities along a fire disturbance gradient were explained by reference to differences in fire tolerance and competitive vigor. Differences in frequency and season of fire produced four distinct plant communities which, when viewed as communities distributed over the landscape, resulted in relatively high beta diversity.

Land managers are faced with increasingly complex problems as the concept of multiple resource management expands to include compositional, structural, and functional biodiversity. Our increased understanding of the "natural" or historical role of fire in shaping forested ecosystems should enable us to better incorporate the use of fire in the management of whole landscapes to accomplish multiple resource objectives.

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